

On the Cranial Osteology of the Fishes of the Families *Osteoglossidæ*, *Pantodontidæ*, and *Phractolæmidæ*. By W. G. RIDEWOOD, D.Sc., Lecturer on Biology at St. Mary's Hospital Medical School, London.

[Read 19th January, 1905.]

(PLATES 30-32.)

AN extensive investigation on the structure of the skull of the lower Teleostean fishes which I began in the year 1896 has now arrived at a stage of progress that warrants the publication of certain of the results. Two papers have already appeared: one, on the skull of the Elopidae and Albulidae, in the 'Proceedings of the Zoological Society' (1904, ii. pp. 35-81), and the other, on the skull of the Mormyridæ, Notopteridæ, and Hyodontidæ, in the 'Journal of the Linnean Society' (Zoology, xxix. 1904, pp. 188-217). The present communication represents a third instalment of the results; a fourth, dealing with the skull of the Clupeoid fishes, is rapidly approaching completion.

Seven species of fishes are considered in this paper—three species of *Osteoglossum*\*, and one species of each of the genera *Arapaima*, *Heterotis*, *Pantodon*, and *Phractolæmus*. These fishes are all of freshwater habit, they are all tropical, and, with the exception of *Osteoglossum Leichardti* of Queensland, all occur within ten degrees of the Equator. *Osteoglossum bicirrhosum* and *Arapaima gigas* are found only in Brazil and Guiana, *Osteoglossum formosum* in Borneo and Sumatra, and *Heterotis niloticus*, *Pantodon Buchholzi*, and *Phractolæmus Ansorgii* in Equatorial Africa.

One of the most striking and characteristic features of the skull of the Osteoglossid fishes is the occurrence of a paired lateral peg of the parasphenoid bone for articulation with the hyopalatine arch, described by Bridge in *Osteoglossum formosum*

\* The Australian species of *Osteoglossum* was described by Günther in 1864 under the name of *Scleropages*, but he afterwards withdrew the genus, considering his *Scleropages Leichardti* to be a species of *Osteoglossum*. Boulenger, however (Ann. Mag. Nat. Hist. (7) viii. 1901, pp. 514-515), has recently found that *Osteoglossum bicirrhosum* differs from *O. formosum* and *O. Leichardti* in the number of vertebræ, the position of the pelvic fins, and the number of branchiostegal rays, and he proposes to re-establish the genus *Scleropages* for the inclusion of the latter two species.

(Proc. Zool. Soc. 1895, pp. 302–310). When, during the course of the investigation, it was found that this articulation occurred in *Arapaima* and *Heterotis* and in *Osteoglossum bicirrhosum* and *Osteoglossum Leichardti*, as well as in *Osteoglossum formosum*, it became of interest to ascertain whether it was present in *Pantodon* and *Phractolæmus*, isolated genera belonging to families of their own, but usually associated with the Osteoglossidæ. As is shown in the sequel, the articulation is present in *Pantodon*, but not in *Phractolæmus*.

I have to acknowledge my indebtedness to Mr. G. A. Boulenger for offering to me facilities for the examination of the skulls of *Pantodon*, *Phractolæmus*, *Arapaima*, *Heterotis*, and *Osteoglossum bicirrhosum* in the British Museum collection, and to Prof. G. B. Howes and Prof. T. W. Bridge for the loan of skulls of *Osteoglossum Leichardti* and *Osteoglossum formosum* respectively.

#### O S T E O G L O S S I D Æ.

##### O S T E O G L O S S U M.

Figures of the top and side of the skull of *Osteoglossum formosum*, and a few words of explanation, are given by Müller and Schlegel (Temminck's Verh. Nat. Ges. Nederl. overz. bez., Zool., Leiden, 1839–44, Pisces, pl. i. figs. 2 & 3, and pp. 5 & 6). A few remarks on the skull-bones of the same species of *Osteoglossum*\* are included in Hyrtl's account of the skull of *Heterotis Ehrenbergi* (Denkschr. Akad. Wiss. Wien, viii. 1854, pp. 73–76). Bridge's account of the skull (*Osteoglossum formosum*, Proc. Zool. Soc. 1895, pp. 302–310), though more detailed, is incomplete, being limited to "certain features," notably the articulation between the parasphenoid and the hyopalatine arch.

##### O S T E O G L O S S U M L E I C H A R D T I.

The skull here described is one specially prepared for the purposes of this investigation from a specimen belonging to the Royal College of Science, London.

*Cranium* (Pl. 30. figs. 1, 2, and 3).—The parietal bones touch one another in the median line of the head. The surface of the anterior two-thirds of each is sculptured, the posterior third lies at a lower level and is not sculptured. The frontal bones are

\* The species is identified as *formosum* by Boulenger (Ann. Mag. Nat. Hist. (7) viii. 1901, p. 514).

relatively short; they do not extend over the ethmoid region, the enlarged nasals constituting the roofing-bones of this part of the cranium. The nasals are important bones, suturedly united with the frontals, with the mesethmoid, and with one another, and also united by their edges with the preorbitals and premaxillæ. They cover the prefrontals completely.

The mesethmoid is a small rhombic bone of ectosteal origin. The nasal, frontal, and mesethmoid bones, and the upper portion of the squamosal are sculptured. The opisthotic is comparatively large; its ventro-lateral angle is united with a backwardly directed process of the pro-otic. The postfrontal does not present itself in a dorsal view of the skull, but is covered by the frontal, squamosal, and postorbital bones. Neither orbito-sphenoid nor basisphenoid bone is present.

The lateral temporal groove is partially roofed over by a lateral growth of the squamosal. The margin of the posterior temporal fossa is bounded by the epiotic and squamosal, these bones uniting both above and below it. The vacuity passes forwards and slightly inwards, but does not end blindly in front; it curves outwards and opens laterally into the lateral temporal groove between the postfrontal and squamosal. This aperture appears at first glance to correspond with the "temporal foramen" of the Clupeoids; but it must be remembered that the latter foramen leads directly into the cranial cavity, and is bounded by the parietal and frontal bones. The subtemporal fossa, lying immediately below the squamosal portion of the articular facet for the head of the hyomandibular, is a fairly large pit, bounded by the pro-otic, exoccipital, opisthotic, and squamosal.

A rod-like process of the parasphenoid rises on each side to meet the alisphenoid, but it does not reach the postfrontal, as it does in *Osteoglossum formosum* (Bridge, *l. c.* p. 302 and pl. 22. fig. 1). From the lower part of this process of the parasphenoid there projects a lateral peg-like outgrowth which articulates with the entopterygoid and hyomandibular. A small clump of strong teeth is situated on the ventral side of the parasphenoid just behind the articulation, and these teeth, together with those of the two entopterygoids, engage with the lingual teeth borne by the median constituents of the hyobranchial skeleton. The parasphenoid extends a little more posteriorly than the basi-occipital. The eye-muscle canal does not open posteriorly; there is a distinct hole behind the parasphenoidal teeth, but this

ends blindly in front. The front of the vomer bears two large teeth and a few smaller ones.

*Temporal and Preopercular Series*\* (Pl. 30. figs. 4 and 5).—The body of the post-temporal is small and horizontally disposed, and its sensory canal is continued forwards into the supratemporal. It has two limbs, nearly equal in length—a superficial one to the top of the epiotic, and a deep, more rod-like one to the back of the opisthotic. The supratemporal is a curved tubular bone, lying close behind the transverse crest of the squamosal and parietal, with which bones it is in close fibrous union.

The preopercular is sculptured in its lower part, but not in its upper part, which is overlapped by the postorbital plates. The lower limb of the preopercular is not quite half as long as the upright limb, and makes with it an angle of rather less than a right angle. The interopercular lies on the inner surface of the preopercular and is not sculptured.

*Circumorbital Series* (fig. 4).—In addition to the nasal bone, which has already been considered in dealing with the cranium, there are six bones of the circumorbital series. They are all sculptured. The two postorbitals are very large, and the preorbital and suborbital are closely bound by fibrous tissue to the upper edge of the maxilla.

*Maxillary Series* (fig. 4).—The premaxillæ are small in size: they are not freely movable, but are closely connected by their posterior edges with the front of the mesethmoid and nasal bones. They carry four or five teeth each. The maxillæ are long bones extending nearly as far back as the mandibular articulation. Each bears a single row of 35 to 40 sharply conical teeth, which diminish in size from before backwards. Both premaxilla and maxilla are sculptured. There is no surmaxilla.

*Mandibular Series* (figs. 4 and 5).—The dentary is long, with a single row of about 35 teeth, diminishing in size from before backwards. The angular is distinct from the articular, and a sesamoid articular is present. The exposed parts of the dentary and articular are sculptured. The articular facet for the head of the quadrate is formed by the articular alone.

\* The reasons for including the preopercular and interopercular bones in this series, and for excluding them from the opercular and branchiostegal series, are given in a former paper (Proc. Zool. Soc. 1904, ii. pp. 68 & 75). For reasons given in the same paper it is considered expedient to regard the post-temporal as a constituent of the skull.



*Hyopalatine Series* (fig. 5).—The hyomandibular articulates with the cranium by a single head, broad antero-posteriorly. Its anterior edge is continued down to meet the upper part of the entopterygoid, and the lateral process of the parasphenoid lies just below and behind the junction. There is here a definite articulation between the parasphenoid and the hyopalatine arch, permitting a certain amount of lateral play to the latter, but preventing any antero-posterior movement. The process of the parasphenoid is so firmly fixed between the hyomandibular above and the entopterygoid below, that it is not easy to remove the hyopalatine arch from the rest of the skull without fracturing one or other of these bones. The metapterygoid just fails to reach the articulation.

A flat lamina of the inner part of the symplectic spreads forward over the metapterygoid and quadrate. There is no separate palatine bone; the palatine cartilage is unossified, and the ectosteal palatine is indistinguishably fused with the ectopterygoid. The palatine cartilage is connected with the ethmoid region of the cranium by a single terminal head, but the connection is of a ligamentous, rather than of a synovial character. Crowded teeth occur on the ectopterygoid and palatine. The entopterygoid sends forward a slender process which nearly reaches the front of the palatine; it bears numerous crowded teeth over nearly the whole of its buccal surface, the largest teeth being those nearest the median plane of the head. I cannot agree with Bridge (*l. c.* p. 305) in his contention that by means of the parasphenoidal articulation of *Osteoglossum* the teeth along the mesial edges of the two entopterygoids are enabled to grip food-material as by the action of right and left jaws, working inwards and outwards. The teeth in question are certainly obliquely set, as he states, but their points are directed vertically downwards. There can be no question that these teeth act in a vertical direction, and are opposed to the lingual teeth borne upon the bone that covers the glossohyal cartilage and the basibranchials.

*Opercular Series* (figs. 4 and 5).—The opercular bone is large and nearly semicircular in outline. The subopercular is small and is sculptured in its posterior part only. The number of branchiostegal rays of *Osteoglossum Leichardti* is stated by Boulenger (*l. c.* p. 515) to be 15–17. In the specimen now

under consideration there are ten only, but the series is probably incomplete\*.

The first seven have the form of curved thin rods, the last three are larger and broader. The first eight are connected with the outer surface of the ceratohyal, the other two with the outer surface of the epihyal.

*Hypobranchial Series.*—The hypohyal is single on each side, and is attached to the upper half of the anterior extremity of the ceratohyal. The anterior end of the urohyal lies between the lower halves of the anterior ends of the right and left ceratohyals. The urohyal is comparatively small, and does not extend back behind the middle of the second basibranchial. A large dentigerous bone overlies the glossohyal cartilage, the first and second basibranchial bones, and the anterior half of the third. From the mesial edge of the ventral side of the anterior end of the second hypobranchial there descends a stout process of rod-like form, almost equalling in length the hypobranchial itself. The first pharyngobranchial is cartilaginous and there is no spicular bone.

#### OSTEOGLOSSUM BICIRRHOSUM.

The skull examined is that belonging to a skeleton in the British Museum, labelled "1890.2.25.60, Brazil."

The frontal bones are longer than in *Osteoglossum Leichardti*, and the nasals are shorter, while the mesethmoid is quite diminutive. The prefrontals appear to be unossified. The posterior temporal fossa does not open into the lateral temporal groove. The ascending wing of the parasphenoid enters into relation with the postfrontal, as in *Osteoglossum formosum* (Bridge, *l. c.* p. 302). The dentition, as a whole, is less robust than that of *O. Leichardti*, and the clump of teeth on the parasphenoid is smaller. The ventral surface of the anterior half of the parasphenoid is strongly grooved, whereas in *O. Leichardti* it is flat.

There is a distinct third, or supratemporal, limb to the post-temporal, whereas in *O. Leichardti* this is barely recognisable. The opening by which the sensory canal comes to the surface of the preopercular bone occurs higher up that bone in *Osteoglossum bicirrhosum* than in *O. Leichardti*. The premaxilla bears 10 or 11 teeth, and the maxilla, which is conspicuously longer and more slender than that of *O. Leichardti*, carries 64 to 68 teeth.

\* In another specimen (No. 92.1.14.37) there are 13 rays.

The dentary, also, is longer and more slender, and carries 64 or 65 teeth. The sculpturing of the maxillary and mandibular bones is less obvious than in *O. Leichardti*.

The parasphenoid-hyopalatine articulation concerns the entopterygoid, not the metapterygoid. The branchiostegal rays in the specimen examined are eight on each side; but Agassiz (Spix, Pisc. Bras.), Günther (Brit. Mus. Cat. Fishes, vii. p. 378), and Boulenger (Ann. Mag. Nat. Hist. (7) viii. 1901, p. 514) put the number at ten. The third pharyngobranchial is considerably stouter than in *O. Leichardti*.

#### OSTEOGLOSSUM FORMOSUM.

Seeing that in *Osteoglossum Leichardti* and *O. bicirrhosum* the parasphenoidal pegs articulate with the entopterygoid, whereas Bridge described the articulation as taking place with the metapterygoid in *O. formosum*, I was particularly anxious to examine this last species, and Prof. Bridge was good enough to lend me the skull which in 1895 he described in the 'Proceedings of the Zoological Society.'

The skull is in many respects intermediate between those of *O. Leichardti* and *O. bicirrhosum*. The nasal is more sculptured than in the latter, but the size of the nasal relatively to the frontal is more like that of *O. bicirrhosum* than that of *O. Leichardti*. The prefrontal is ossified. The posterior temporal fossa does not open into the lateral temporal groove.

The cluster of teeth on the parasphenoid is smaller than in *O. bicirrhosum*, and the two posterior teeth are much larger than the other 10 or 12. The appearance of this cluster is well shown in Bridge's figs. 1, 2, and 4. The ventral surface of the front half of the parasphenoid is grooved. Teeth are present on the vomer. There are 10 or 11 teeth on each premaxilla, and about 50 on each maxilla, while each dentary carries about 52 teeth. The jaw-bones are longer than those of *O. Leichardti*, but not so long as those of *O. bicirrhosum*.

The parasphenoidal articulation is with the entopterygoid, and not the metapterygoid as described by Bridge. On returning to Prof. Bridge the skull which he was good enough to lend me for examination, I pointed this out, and received in reply an admission that he now regarded the articulation as really entopterygoidal.

The preopercular is intermediate in character between those

of *O. Leichardti* and *O. bicirrhosum*. The branchiostegal rays are 14 or 15 in number on each side: according to Müller and Schlegel (Temminck's Verh. Nat. Nederl. overz. bez., Zool., Leiden, 1839-44, Pisces, p. 7) the number is 15; Hyrtl (Denkschr. Akad. Wiss. Wien, viii. 1854, p. 76) says 17; Günther (Brit. Mus. Cat. Fish. vii. 1868, p. 378) says 15; Boulenger (Ann. Mag. Nat. Hist. (7) viii. 1901, p. 515) says 15-17.

#### HETEROTIS NILOTICUS.

Hyrtl (Denkschr. Akad. Wiss. Wien, viii. 1854, pp. 73-76, three plates) has published a side view of the skull of *Heterotis*, and a moderately good description, not sufficiently detailed, however, to be of much real service. An account of the hyobranchial skeleton is also given, and his figures of the epibranchial organ, the shape of which he compares with that of the shell of *Planorbis*, show well the peculiar features of this remarkable structure.

Views of the skull, gills, and epibranchial organ are also given by Hemprich and Ehrenberg (Symbolæ Physicæ, zootomical plates 8 and 9, 1899).

The skull described below is that of a skeleton in the British Museum. It is marked "Kartoum," but bears no register number.

*Cranium* (Pl. 31. figs. 6, 7, and 8.)—The nasal bones are large and are incorporated into the cranium; they meet one another in a median suture, and are suturally united with the frontal bones. The mesethmoid is small, and appears on the dorsum of the cranium between the anterior ends of the nasal bones. The frontals are large and broad; the parietals are comparately large and meet in a median suture. The nasal, frontal, squamosal, and parietal bones are sculptured, but the hindermost parts of each parietal and squamosal lie at a deeper level and are not sculptured. Shallow unsculptured depressions, each with a perforation by which the sensory canal comes to the surface of the head, occur on the nasal, frontal, parietal, and squamosal bones in the positions shown in fig. 6. The supraoccipital is small and has a feeble crest, and the posterior part of the cranium lying beneath the supraoccipital and above the foramen magnum is cartilaginous (fig. 8).

The occipital half-vertebra comes away readily from the exoccipitals and basioccipital, and leaves their posterior ends rough. It has a complete neural arch, but no neural spine; it bears a



pair of intermuscular bones, and a pair of large ribs\*, which are attached to the upper ends of the clavicles. This half-vertebra is not shown in figs. 6, 7, and 8, but a separate view of it is given in fig. 11. Since both the ribs and the intermuscular bones slope backward as well as outward, they appear in the figure shorter than they really are. These ribs are shown at *a* in Hyrtl's pl. 2. fig. 1; the bones marked *b* are the ribs of the next vertebra but one, a fact which one would not gather from an examination of his figure, nor from his description of them (p. 88) as "das erste Rippenpaar."

The opisthotic is fairly large, and extends forward to meet the pro-otic, but above the junction of the opisthotic with the pro-otic there is no subtemporal fossa. The posterior temporal groove is not well marked, although in *Arapaima* and *Osteoglossum* there is a completely roofed posterior temporal fossa; the lateral temporal fossa is roofed over by the squamosal bone to a greater extent than in *Osteoglossum*. The side view of the skull shows a large foramen between the exoccipital and basioccipital, bounded mainly by the former bone; it is apparently the vagus foramen, much larger than usual. The postfrontal is fairly large; the prefrontal is of moderate size. These bones are not sculptured, being covered by bones of the circumorbital series.

The cranial cavity extends forward through, and in front of, the orbital region, so that the membranous interorbital septum is reduced to a small tract between the alisphenoids and the parasphenoid. The two alisphenoids meet along their ventral edges in a median suture, and the hinder end of this suture meets an upwardly directed process of the parasphenoid. The orbitosphenoid is a broad, imperfectly ossified sheet of cartilage, U-shaped in section. It rests upon the parasphenoid, and is united with the prefrontals anteriorly, with the alisphenoids posteriorly, and with the frontals above.

There appears to be no basisphenoid. The eye-muscle canal does not open posteriorly. Neither the vomer nor the parasphenoid bears teeth. The parasphenoid divides posteriorly into

\* Although a pair of strong intermuscular bones pass from the occipital half-vertebra to the upper ends of the clavicles in *Chanos*, they are not homologous with the bones now under consideration, which arise lower down the side of the half-centrum and are in serial order with the ribs. The resemblance in the two cases is curious, but it is not one of homology.

two slender points which lie closely bound to the right and left sides of the anterior half of the basioccipital. Just in front of the pro-otic region a pair of strong oblique processes extend from the parasphenoid outward, forward, and downward, for articulation with the entopterygoid.

*Temporal and Preopercular Series* (figs. 9 and 10).—The post-temporal has an upper limb the anterior extremity of which overlies the epiotic, and a deep, rod-like limb attached by ligament to the posteriorly directed process of the opisthotic. The horizontal sensory canal lies towards the ventro-external part of the body of the post-temporal bone, and the bony tube surrounding the canal is continued forward towards the supratemporal, but fails to reach it. The supratemporal is rather small, and is partly wedged in beneath the postero-lateral margin of the parietal. It is not a sculptured bone.

The lower part of the preopercular is sculptured. The lower limb is nearly as long as the upright portion, and makes with it an angle of rather less than a right angle. The interopercular is a thin flake of bone, of large size, lying on the inner surface of the lower part of the preopercular.

*Circumorbital Series* (fig. 9).—In addition to the nasal bone, previously mentioned, there are five bones of this series. The preorbital bone has a prominent ridge running upwards along its inner surface. The largest of the series is the postorbital, the anterior edge of which bone is considerably thickened. They are all sculptured.

*Maxillary Series* (fig. 9).—The mouth, when viewed from the front, is curiously square in shape, and the upper side of the square is formed by the premaxillæ. The two premaxillæ are separated by the narrow vomer, so that the middle part of the upper jaw is toothless. Each premaxilla bears about thirteen teeth. The number of teeth in the maxilla is about fourteen, and these, like those of the premaxilla, are long, blunt, and curved at the tips. The maxilla, when isolated, is seen to be bent at its middle into a right angle. The horizontal part lies over the premaxilla and is toothless; it nearly reaches the vomer, but does not enter into definite relation with it and has no articular head. There is no surmaxilla.

*Mandibular Series* (figs. 9 and 10).—The dentary rises high, and the coronoid process is set well forward. The teeth are similar to those of the premaxilla, and are about twenty-two

in number. The articular does not rise very high, and forms no part of the coronoid process. The endosteal articular does not appear to be readily separable from the ectosteal articular; there is a small sesamoid articular. The angular bone is distinct from the articular, and forms the lower part of the articular facet for the head of the quadrate.

*Hyopalatine Series* (fig. 10).—The hyomandibular articulates with the cranium by two barely separated heads, the anterior of which is smaller than the other and rises higher. The opercular head is stout. The hyomandibular enters into sutural relation with the preopercular as well as the metapterygoid along its ventral edge; it sends a slender process forward to meet the entopterygoid. As in *Osteoglossum*, a lateral process of the parasphenoid articulates with the back of the entopterygoid just beneath this process of the hyomandibular. The part of the entopterygoid that lies below and in front of the articulation carries an oval patch of crowded teeth, straight and rather blunt. It is worthy of note that Valenciennes alludes incidentally to this articulation between the hyopalatine arch and the parasphenoid (*Hist. Nat. Poiss.* xix. 1846, p. 471).

The ectopterygoid is slightly curved, and is not continued down the anterior edge of the quadrate. The relations of the palatine are rather strange, for the entopterygoid and ectopterygoid both extend to the anterior end of the hyopalatine arch, while between their anterior portions, and confluent with them, lies an extremely delicate membrane-bone, apparently to be identified as the palatine, bearing on its upper surface, at some distance from the front, the conical endosteal palatine. The palatine and ectopterygoid are edentulous.

*Opercular Series* (figs. 9 and 10).—The opercular bone is of average size and shape. The subopercular is wanting on both sides in the specimen under observation, but it is important to note that Valenciennes (*Hist. Nat. Poiss.* xix. 1846, p. 470) has described a small subopercular in the following terms:—"Le sous-opercule est représenté ici par une toute petite pièce osseuse, mince comme une écaille et située dans le petit espace angulaire que laissent entre eux l'opercule et le préopercule. J'insiste sur la petitesse de cet os, parce qu'il est très-facile de l'enlever et de le perdre dans l'épaisseur du bord membraneux de l'opercule en préparant le squelette du poisson, et j'avertis qu'il faut l'avoir vu sur le squelette pour le retrouver sur le poisson desséché."

The branchiostegal rays are eight in number on each side. Of

these, four are on the ceratohyal, one lies on the junction between the epihyal and the ceratohyal, two on the lower edge of the epihyal, and the last one about halfway up the outer face of the epihyal. The first five are slender rods, the other three are lamellate. The last of all, which is the largest, tends to remain on the inner surface of the interopercular when the head is dissected prior to the maceration of the bones. Rüppell (Besch. neu. Nil-Fische, 1829, p. 11) puts the number of branchiostegal rays of *Heterotis* as 7, as also do Hyrtl (Denkschr. Akad. Wiss. Wien, viii. 1854, p. 75) and Boulenger (Ann. Mag. Nat. Hist. (7) viii. 1901, p. 515); Valenciennes (*l. c.* p. 471) and Günther (Brit. Mus. Cat. Fishes, vii. 1868, p. 380) say 8. Eight are shown in pl. 8 (zootom.), fig. 2 of Hemprich and Ehrenberg (*Symbolæ Physicæ*, 1899).

*Hyobranchial Series.*—The hyobranchial skeleton of the specimen examined is incomplete. The urohyal is short and stout and lies between the strongly-developed processes that project downward from the anterior ends of the second hypobranchials. There is a small upper hypohyal, but no lower. The basibranchial teeth, which are not quite so large as those of the entopterygoid, are arranged in a patch, about as broad as long, set on the middle part of the length of the membrane-bone that covers the hinder part of the glossohyal, the whole of the first and second basibranchials and the anterior three-fourths of the third. The epibranchial organ is borne by the fourth and fifth arches.

The glossohyal, the first basibranchial, and the first pharyngobranchials appear to be cartilaginous, and there are no spicular bones. According to Cope (Trans. Amer. Phil. Soc. n. s. xiv. 1871, p. 455) there are but two superior pharyngeals in *Heterotis*, whereas in *Osteoglossum* there are three. Seeing that in both *Osteoglossum* and *Heterotis* the first pharyngobranchial is unossified, the only explanation of the statement lies, I think, in the fact that Cope, in examining *Osteoglossum*, mistook for a pharyngobranchial the patch of coalesced teeth that lies behind the third pharyngobranchial, and immediately beneath that cartilaginous rod which represents the fourth pharyngobranchial. The dentigerous plate in question is wanting in *Heterotis*.

#### ARAPAIMA GIGAS.

The only published figures and description of the skull of *Arapaima* are those of Agassiz (Spix, *Selecta Genera et Species Pisc. Bras.* 1829, pl. B of the Anatomical Plates, and pp. 33-40).



The bones are numbered and are referred to in detail in the text. A copy of the uppermost figure of the plate was republished in 1844 without the numbers (Agassiz, Monog. Poiss. Foss. Vieux Grès Rouge, 1844-45, pl. F: see also pp. 107-109 of the text). The relations of the sculptured to the non-sculptured parts of the head are well shown in the figures given by Valenciennes (Hist. Nat. Poiss. xix. 1846, pls. 579-582).

Two skulls of *Arapaima* were available for study—a small incomplete skull measuring 7 inches in length, and a full-sized skull, about 16 inches long, forming part of an articulated skeleton exhibited in the British Museum. The details of the cranium, hyopalatine arch, and mandible were made out from the small specimen, and figs. 12, 13, 14, and 16 were drawn from this; fig. 15, showing the superficial bones, was drawn from the larger specimen.

*Cranium* (Pl. 32. figs. 12, 13, and 14).—The parietals are large, and meet one another in the median line along their whole length. The squamosals appear rather small as compared with the parietals. The nasals are of considerable size and are incorporated into the cranium; they meet one another in a median suture, and are suturally united with the anterior edges of the frontals. The nasal, frontal, parietal, and squamosal bones are sculptured on their upper surface, but each has a shallow depression devoid of sculpturing, at the bottom of which is a perforation where the tubes of the sensory canal-system come to the surface. A median depression of a similar nature occurs in the postero-mesial parts of the parietal bones, just in front of the supraoccipital. The posterior, deep-lying part of the parietal is relatively much smaller than in *Osteoglossum*, and forms but a small semicircular lamina overlying the base of the epiotic prominence. Neither the prefrontal nor the postfrontal comes to the surface of the head, and neither is sculptured.

There is a backwardly directed supraoccipital crest of small size. The vagus foramen in the middle of the side of the exoccipital is large, and in the part of the exoccipital bone which forms the side of the foramen magnum there are three foramina, as in *Osteoglossum*. The opisthotic is of moderate size; it is united with the epiotic, exoccipital, and squamosal, and with a backward prolongation of the pro-otic. A lateral depression occurs in the upper part of the pro-otic bone; the subtemporal fossa is ill-defined and shallow. The posterior temporal fossa is

completely roofed; its aperture is triangular in the small specimen, but rounded in the large one; it is bounded by the epiotic, opisthotic, and squamosal. Its anterior blind end is limited by the supraoccipital, parietal, and squamosal bones.

The occipital half-centrum presents a shallow concavity behind, and is readily separable from the basioccipital and exoccipital bones. The vertebral centrum behind this may also be regarded as a constituent of the cranium, since its lower portion is continued forward into two parallel processes, right and left, which are rigidly united by long jagged sutures with the back of the parasphenoid. The parasphenoid bears a long patch of crowded small teeth, and from its lateral edges there project, as in *Osteoglossum* and *Heterotis*, a pair of strong processes which enter into definite articulation with the entopterygoids. Each lateral process of the parasphenoid projects slightly forward, and is covered by synovial cartilage on its anterior edge. The vomer is a flat bone, bearing crowded small teeth similar to those of the parasphenoid. The mesethmoid is almost entirely cartilaginous; there is a small median endosteal ossification lying between the nasals above and the vomer below, but it does not present itself on the surface of the skull.

The orbitosphenoid is a paired bone of small vertical extent, in contact with the frontals above and the parasphenoid below. The orbitosphenoids reach the prefrontals in the large specimen, but not in the smaller; they are apparently separated from the alisphenoids behind. Unfortunately the alisphenoids are missing from both specimens, as also is the basisphenoid bone.

*Temporal and Preopercular Series* (fig. 15).—The post-temporal consists of a curved flake of bone continued forward into a point which rests over the epiotic prominence. The sensory canal traverses its lateral edge horizontally; the deep or opisthotic limb is well developed and is almost as long as the epiotic limb. The bone is not sculptured. In the larger specimen, owing to the forward spreading of the bone diminishing the space between the epiotic and opisthotic limbs, these limbs appear shorter than in the smaller specimen.

The horizontal limb of the preopercular is about as long as the upright limb, and makes an angle of 90 degrees with it. The strong development of the horizontal limb of the preopercular, taken in conjunction with the slope of the hyomandibular, points either to a reduction in the length of the gape, or to an increase

in the length of the postorbital portion of the head; the latter is the more probable supposition. The interopercular is a large, flat lamina of bone; it lies hidden by the lower part of the preopercular and is not sculptured.

The supratemporal differs considerably in shape and relative size in the two skulls. In the smaller skull it is a small bone which fits into the depression between the posterior ends of the parietal and squamosal. Only a small portion of it is superficial and sculptured, and the tubular portion that carries the sensory canal is continued backward to about the same transverse level as the tip of the epiotic prominence. In the larger specimen the supratemporal is of fair size; it projects downward and outward from the parietal and squamosal so as nearly to reach the upper edge of the opercular bone, and its anterior edge unites by a serrated suture with the posterior edge of the upper of the large postorbital plates.

*Circumorbital Series* (fig. 15).—The nasal bones have already been mentioned in dealing with the cranium. The orbital ring is complete and consists of five bones. The preorbital forms the anterior half of the upper border of the orbit, and the uppermost of the postorbitals the posterior half; the other two postorbitals are very large cheek-plates; there is one suborbital. These bones are all sculptured except in certain elliptical areas, within each of which is an opening for the sensory canal.

*Maxillary Series* (fig. 15).—The gape is bounded above by both premaxilla and maxilla, the former bearing 16 or 18 teeth and the latter from 30 to 35 teeth, arranged in a single row. The teeth are uniform in size, and are rather cylindrical in shape, somewhat laterally compressed, with very slight curvature and with bluntly conical tips. The posterior part of the premaxilla is overlapped by the nasal in such a manner as to suggest that there is no freedom of movement between these bones. The edentulous portion of the maxilla that lies along the postero-ventral surface of the premaxilla is long and tapering, and extends as far as the median plane of the head. The extremities of the two maxillæ thus meet one another behind the premaxillary symphysis, but they do not themselves unite in any definite manner. The exposed part of the premaxilla is sculptured, but the maxilla exhibits no sculpturing, or just a little near the roots of the teeth. There is no surmaxilla.

*Mandibular Series* (figs. 15 and 16).—The coronoid process

has the form of a thin vertical plate with concave upper border; it is constituted mainly by the dentary, but the ectosteal articular forms the posterior extremity. The endosteal articular and the ectosteal articular are distinct and separate readily. The articular surface for the quadrate is formed mainly by the endosteal articular, but partly also by the angular, which is a separate bone. There is no sesamoid articular. The ventrolateral surfaces of the angular, ectosteal articular, and dentary are sculptured.

The dentary bears a single row of about 30 teeth similar in form and size to those of the maxilla. The bone is very complete on the inner or lingual side of Meckel's cartilage, and bears one, two, or three elliptical patches of small teeth in the position shown in fig. 16 at *s*. These teeth were noticed by Valenciennes, who wrote concerning them:—"Au côté interne de chaque branche de la mandibule je vois, sur une assez large plaque triangulaire, un groupe de fines scabrosités ou de petites dents, semblables à celles des palatins" (Hist. Nat. Poiss. xix. 1846, p. 446). Although the bony lamina that bears the teeth occupies the position of the splenial bone, it is not a distinct plate of bone as might be concluded from the remark of Owen (Anat. of Vert. i. p. 123)—"The *Sudis*, fig. 88 \*, the *Polypterus*, and *Amia*, have the splint-like plate along the inner surface of the ramus, called 'splenial'; it supports teeth and develops a coronoid process." The passage continues:—"In both *Sudis* and *Lepidosteus* there is superadded a small bony piece, *ib.* 29 *a*, answering to the surangular in Reptiles." This bone, marked 29 *a*, is, I believe, merely the endosteal articular displaced.

*Hyopalatine Series* (fig. 16).—The head by which the hyomandibular articulates with the cranium is indistinctly divided into a small front head and a large hinder one, broad anteroposteriorly. The head that articulates with the opercular bone is long drawn out, and on the external face of the hyomandibular there is a short projection that engages with the anterior edge of the upper part of the preopercular. The axis of the hyomandibular slopes more forward than downward. The metapterygoid is of average size, but only a small portion of it is visible in the buccal aspect of the hyopalatine arch. The symplectic is large and of curious shape, since it throws out jagged-edged laminae

\* Fig. 88 represents the disarticulated mandible of *Arapaima gigas*.



towards the hyomandibular, metapterygoid, quadrate, and preopercular. The thickened axis, however, can be recognized, and this makes an angle of about 50 degrees with the horizontal plane.

Projecting from the back of the quadrate is a considerable lamina of bone (apparently membrane-bone) which flanks the outer surface of the lower part of the symplectic and lies just above the horizontal limb of the preopercular. The ectopterygoid is not bent, and is indistinguishably united with the palatine. In this feature, and in the absence of any endosteal part of the palatine, *Arapaima* resembles *Osteoglossum*. The buccal surfaces of the pterygoid and palatine bones are almost completely covered with densely crowded small teeth. The lateral process of the parasphenoid, already referred to, fits into an elliptical foramen bounded above and behind by the hyomandibular, below by the hyomandibular and metapterygoid, and in front by the entopterygoid. The synovial articulation is with the entopterygoid.

*Opercular Series* (fig. 15).—The opercular bone is of average proportions; it is nearly semicircular in outline, and is sculptured over the whole of its outer surface except near the upper and anterior edges. The subopercular is small, triangular, and not sculptured. There are ten or eleven branchiostegal rays, of which five or six are attached to the ceratohyal, and the remainder to the epihyal. They constitute an evenly graduated series; the front ones have the form of slender curved rods, the hinder ones are larger, and slightly expanded and lamellate. Agassiz (Spix, Pisc. Bras. 1829, Anat. Plate B, fig. 5) shows ten rays; Valenciennes (Hist. Nat. Poiss. xix. 1846, p. 438), Günther (Brit. Mus. Cat. Fishes, vii. 1868, p. 376), and Boulenger (Ann. Mag. Nat. Hist. [7] viii. 1901, p. 515) are agreed in putting the number at sixteen.

*Hyobranchial Series*.—In neither of the specimens available is the hyobranchial skeleton complete. The interhyal is ossified. There is a single hypohyal on each side, and this is probably the equivalent of the lower of the two that are present in so many other Teleostean fishes. The first, second, and third basibranchials are overlaid by a readily removable dentigerous plate of the form of a greatly elongated ellipse, the teeth of which are densely crowded and similar to those of the parasphenoid and pterygoid bones. Behind this is a small circular dentigerous bone of similar character.

SUMMARY AND COMMENTS ON THE SKULL IN THE  
FAMILY OSTEOGLOSSIDÆ.

A review of the craniological characters of the three genera *Osteoglossum* (with *Scleropages*), *Heterotis*, and *Arapaima* shows that they constitute a perfectly natural group. In shape and general appearance the skulls vary considerably, but in the more fundamental and essential features they are similarly constructed.

In all three, the superficial parts of the bones are sculptured. The parietal bones meet in the median line, and, as in the widely remote genus *Erythrinus*, the deeper-lying, muscle-covered hinder portion of each is not sculptured. The frontal bones are relatively short and broad in *Osteoglossum* and *Heterotis*, but in *Arapaima*, with its elongated head, their proportions are more normal. The nasal bones are large; they meet one another by a median suture, and they are suturally united with the anterior ends of the frontal bones.

The mesethmoid is small in all three genera. The opisthotic is of fair size and touches the pro-otic. A subtemporal fossa similar to that of the Elopidae and Albulidae is found beneath the squamosal portion of the articular surface for the head of the hyomandibular in *Osteoglossum*; in *Arapaima* the subtemporal fossa is wide and shallow, in *Heterotis* it is wanting. The basi-sphenoid is wanting in all three; the orbitosphenoid is a paired bone in *Arapaima*, in *Heterotis* it is an imperfectly ossified trough-like cartilage, in *Osteoglossum* it is wanting. The occipital half-centrum comes away readily from the basioccipital and exoccipital bones, leaving their posterior ends rough, in *Heterotis* and *Arapaima*, but not in *Osteoglossum*; in *Arapaima* the centrum behind the occipital half-centrum sends forward a pair of processes which unite with the hinder part of the parasphenoid.

The posterior temporal groove is completely roofed over in *Arapaima* and *Osteoglossum*, but not in *Heterotis*; indeed, in *Heterotis* the groove is barely recognisable. In all three genera the parasphenoid bears on each side a stout peg which articulates with the entopterygoid. In *Osteoglossum Leichardti* the parasphenoid has an ascending process which reaches the alisphenoid, and in *Osteoglossum bicirrhosum* and *Osteoglossum formosum* the corresponding process reaches the postfrontal. The parasphenoid and vomer bear teeth in *Osteoglossum* and

*Arapaima*, but not in *Heterotis*; the eye-muscle canal does not open posteriorly.

In all three the post-temporal has well-developed epiotic and opisthotic limbs; the orbit is surrounded by five or six bones, of which the postorbitals are the largest. The gape is bounded above by the premaxilla and maxilla; teeth are borne by the premaxilla, maxilla, and dentary; there is no surmaxilla. The angular bone is distinct from the articular; it takes part in the formation of the articular facet for the head of the quadrate in *Arapaima* and *Heterotis*, but not in *Osteoglossum*. The endosteal articular is separable from the ectosteal articular in *Arapaima*, but not in *Osteoglossum* and *Heterotis*. A sesamoid articular is present in *Osteoglossum*, and a small one in *Heterotis*, but it is apparently wanting in *Arapaima*. The symplectic exhibits a tendency to spread over the adjacent bones in *Arapaima* and *Osteoglossum*, but the tendency is less apparent in *Heterotis*. In *Heterotis* there is a distinct palatine bone, but in *Osteoglossum* and *Arapaima* the palatine is not separate from the ectopterygoid. Teeth are borne by the entopterygoid in *Heterotis*, and by the entopterygoid and the combined palatine and ectopterygoid in *Osteoglossum* and *Arapaima*.

The subopercular is small in *Osteoglossum* and *Arapaima*, and very small in *Heterotis*. The branchiostegal rays number 8 on each side in *Heterotis*, 10 or 11 in *Arapaima*, 8 in *Osteoglossum bicirrhosum* (Boulenger, Ann. Mag. Nat. Hist. viii. 1901, p. 514, says 10), 10-13 in *Osteoglossum Leichardti* (Boulenger says 15-17), and 14 or 15 in *Osteoglossum formosum* (Boulenger says 15-17).

The hypohyal is single on each side. A large dentigerous lingual bone is present in *Osteoglossum* and *Arapaima*; in *Heterotis* it is only of moderate size. In *Osteoglossum* and *Heterotis* there is a downwardly directed process of the mesial end of the second hypobranchial, as in Mormyroid fishes; in both of these forms the glossohyal cartilage is unossified, and in *Heterotis* the first basibranchial also, a fact to which Cope attaches some importance (Trans. Amer. Phil. Soc. n. s. xiv. 1871, p. 455). The first pharyngobranchial is unossified and the spicular bone is absent. Cope (*l. c.*) states that the "superior pharyngeals" are three in number on each side in *Osteoglossum*, and two in *Heterotis*; the branchial skeletons of the specimens at my disposal are not sufficiently perfect to enable me to

traverse this statement, but I suspect that the "superior pharyngeal" bone stated to be present in *Osteoglossum* and not in *Heterotis* is the dentigerous plate that underlies the cartilaginous fourth pharyngobranchial.

The deductions that one draws from the above summary are that, so far as craniological characters indicate, the three genera are closely allied, that *Arapaima* is the most primitive of the three, and that there is a closer affinity between *Osteoglossum* and *Arapaima* than between *Heterotis* and either of these forms. It would be of great interest to ascertain whether such of the above characters as are common to *Arapaima*, *Osteoglossum*, and *Heterotis*, more particularly the entopterygo-parasphenoidal articulation, are possessed by the skulls of the extinct *Dapedoglossus* of the freshwater Eocene of Wyoming, and *Brychætus* of the marine Eocene (London Clay) of Sheppey, which genera are included in the family Osteoglossidæ. I have made an inspection of the remains of these fishes in the Geological Department of the British Museum, only to find that the parts most interesting in the present connection are either broken away or are concealed by matrix.

#### TAXONOMIC POSITION OF THE OSTEOGLOSSIDÆ.

Valenciennes (Hist. Nat. Poiss. vol. xix. 1846) placed *Osteoglossum* with *Hyodon*, following immediately after the Mormyroids, which he said they resembled in the structure of their alimentary canal (p. 287). *Arapaima* and *Heterotis* he discussed in consecutive chapters, and the former he regarded as closely allied to *Amia* (p. 439). Johannes Müller ("Bau und Grenzen der Ganoiden," Abhandl. Akad. Wiss. Berl. 1844, p. 190) placed the three genera *Arapaima*, *Osteoglossum*, and *Heterotis* together at the end of his "Clupeidæ," a very large family including not only those fishes which we are now accustomed to regard as "Clupeoid," but also such forms as *Notopterus*, *Amia*, *Alepocephalus*, *Elops*, and *Stomias*.

Günther (Brit. Mus. Cat. Fishes, vii. 1868, p. 377) founded a special family, the Osteoglossidæ, to include the genera *Osteoglossum*, *Arapaima*, and *Heterotis*, and the family has been adopted without alteration in all subsequent schemes of classification, except an admittedly artificial scheme of Cope's (Trans. Amer. Phil. Soc. n. s. xiv. 1871, p. 455), in which the Heterotidæ are associated with the Galaxiidæ, and separated from the



Osteoglossidæ, because of certain characters of the branchial skeleton.

As regards the relations considered by different writers to exist between the Osteoglossidæ and other families of Teleostean fishes, one is not justified in all cases in concluding that the families which are placed nearest to the Osteoglossidæ are regarded by the author as the families most nearly allied to it, for the necessity of treating families in linear series when writing about them tends to obscure many natural relationships of which the author is fully cognisant. It may be noted, however, that the family Osteoglossidæ is placed by Günther (*Study of Fishes*, 1880) between the Clupeidæ on the one hand and the Pantodontidæ, Hyodontidæ, Gonorhynchidæ, Haplochitinidæ, Percopsidæ, and Salmonidæ on the other. Gill (*Smithson. Miscell. Coll.* no 247, 1872, p. 15) gives the following sequence of families:—Characinidæ, Percopsidæ, Haplochitonidæ, Galaxiidæ, Osteoglossidæ, Notopteridæ, Halosauridæ, and Chauliodontidæ; and Boulenger (*Ann. Mag. Nat. Hist.* (7) xiii. 1904, p. 164) the sequence:—Elopidæ, Albulidæ, Mormyridæ, Hyodontidæ, Notopteridæ, Osteoglossidæ, Pantodontidæ, Ctenothrissidæ, Phractolæmidæ, Saurodontidæ, Chirocentridæ, Clupeidæ. Smith Woodward (*Brit. Mus. Cat. Foss. Fishes*, iv. 1901, p. vii) states that the Osteoglossidæ are closely related to the Albulidæ.

The suborder Malacopterygii as restricted by Boulenger (*l. c.* pp. 163–165) consists of a natural assemblage of twenty-one families, beginning with those extinct families that lie on the border-line between the Ganoids and Teleosteans, and ending with specialised families like the Alepocephalidæ, Stomiatidæ, Gonorhynchidæ, and Cromeriidæ. Looking through this list, I should be disposed to associate the Osteoglossidæ with the Pantodontidæ for reasons given on p. 276, and to regard the next nearest family to be the Albulidæ. The conclusion is arrived at by a consideration of the craniological features mainly, but the characters of the other parts of the skeleton and of the soft parts of the body, so far as they are known to me, do not militate against the suggestion that the Osteoglossidæ and Albulidæ have descended from a common stock.

## PANTODONTIDÆ.

## PANTODON BUCHHOLZI.

The small fish known under this name is remarkable for the disproportionately large size of the fins, the shortness of the snout, the large size of the gape, the profusion of teeth, and the reduction of the opercular skeleton. It was first described in 1876 by Peters (Monatsber. Akad. Wiss. Berl. 1876 (1877), pp. 195-200, one plate), who obtained his specimens from Victoria River, in the Cameroons; other specimens have since been obtained from the Congo and Niger. Although the general aspect of the fish resembles that of a Cyprinodont, it is generally admitted (Peters, *l. c.* pp. 198 and 200; Günther, 'Study of Fishes,' 1880, p. 653; Boulenger, 'Poissons du Bassin du Congo,' 1901, p. 120) that its nearest allies are to be found in the Osteoglossidæ. Several of the features of the skull of *Pantodon* have already been recorded in the three works above named.

The skull examined is that belonging to a skeleton in the British Museum, labelled "80.11.24.12, Old Calabar."

The top of the skull is broad and flat, and is divided into four nearly equal parts by the sagittal and parieto-frontal sutures. The parietal bones are large and meet one another in an extensive median suture; the frontal bones are broad, the length of each being not greater than its breadth. The nasals are comparatively large; they are slightly convex above, and are united by suture with the anterior edges of the frontal bones; they do not meet one another in the median line, but are separated by the small mesethmoid. The right and left premaxillæ are fused into a single bone and the suture is obliterated; the bone bears a row of about fourteen small, pointed teeth, and is immovably united with the anterior edges of the nasal bones and mesethmoid. The premaxilla lies in a broad depression in the front edge of the roof of the cranium, with the teeth pointing directly forward; the anterior ends of the maxillary and dentary bones extend in advance of the premaxilla.

None of the bones are sculptured. The prefrontals do not appear on the upper surface of the cranium; the vomer is large, and at its broad front end is a row of teeth, somewhat larger than those of the premaxilla, disposed in the form of a widely-opened V. Beneath that part of the parasphenoid which lies

below the pro-otic bones is a rhomboidal patch of teeth, which terminates anteriorly in a sharp point, and posteriorly in a blunt point. The teeth increase in size from before backward, and the teeth which occur at the hind end of the series are the largest which the fish possesses. On each side of this patch of teeth the parasphenoid is produced into a stout peg, which slopes slightly forward and downward, and articulates with the entopterygoid in the same manner as in the Osteoglossidæ. There are no wings of the parasphenoid ascending towards the post-frontal and alisphenoid; the eye-muscle canal does not open posteriorly.

On each side of the hinder part of the base of the cranium is an inflated bulla of very thin bone, through which may be seen a large otolith. The bulla is formed by the pro-otic, basioccipital, and exoccipital bones. A subtemporal depression, having more the form of a groove running antero-posteriorly than of a fossa, is situated above the level of this bulla, and below the posterior part of the articular facet for the reception of the head of the hyomandibular. There is no auditory fenestra, and there are no diverticula of the swim-bladder contained within the skull. A half-centrum is fused with the exoccipital and basioccipital bones, and the suture between it and the exoccipitals remains visible. The anterior vertebræ are normal, and there are no Weberian ossicles. The posterior temporal depression is not roofed over. A separate opisthotic seems to be wanting. Owing to the great breadth of the orbital region of the cranium, the two alisphenoids are set at a considerable distance apart, and the orbitosphenoid has the form of a widely open **U**, the right and left parts of which are nearly severed. There is no basisphenoid.

The preopercular is a bone of normal size; it has a short horizontal limb, the extremity of which nearly touches the back of the mandible. There is no interopercular. The circumorbital bones are missing from the skull under consideration; but it may be noted that Peters has figured two large postorbital plates, which extend nearly to the edge of the preopercular, and Boulenger writes (*l. c.* p. 120): "La joue est cuirassée par deux grands sous-orbitaires."

The maxilla is long; its anterior extremity projects in advance of the premaxilla, its posterior end is close behind the level of the quadrate-mandibular articulation. The lower edge of the maxilla is toothed from end to end, the teeth being arranged in

two closely approximated rows: the teeth are pointed and exhibit a very slight curvature; they are larger than those of the premaxilla. The front part of the maxilla is rigidly fixed to the outer side of the palatine; there is an important articulation between the maxilla and the under side of the prefrontal, and a slight articulation between the anterior extremities of the maxillary and nasal bones. There is no surmaxilla.

The mandibular ramus is long and slender; the coronoid process is situated very far back, and the upper edge of the dentary is toothed from the symphysis to the base of this process. The teeth are set in two closely-set rows, like those of the maxilla, except that the largest teeth are in the outer row, whereas in the maxilla the largest belong to the inner row.

The hyomandibular articulates with the cranium by a single head. There is no visible suture between the palatine and the ectopterygoid; the entopterygoid extends well forward along the inner edge of the palatine, almost to the extremity of that bone. The entopterygoid is thick in the region of the groove in which the parasphenoidal peg is received, and this part of the bone bears strong, curved, pointed teeth, nearly as large as those on the parasphenoid. Smaller teeth occur on the ectopterygo-palatine bone, a long outer row (really a double row, like the dentition of the maxilla) extending back almost to the quadrate articulation, and a shorter inner row.

The opercular is reduced in size and lies along the upper two-thirds of the preopercular; its width is about two-fifths of its height. There is no subopercular. Several branchiostegal rays are missing from the specimen examined: Peters (*l. c.* p. 196) puts the number as eleven, and Boulenger (*l. c.* p. 120) as nine.

The interhyal is large and ossified; there is a small upper hypohyal, but no lower; the urohyal is very small. Above the glossohyal cartilage and the basibranchials\* is a large, triangular, dentigerous bony plate, concave on its upper surface, recalling the similarly placed lingual bone of *Osteoglossum*, except that the width of the hinder part is greater, and that the largest teeth occur in the median line of the plate. Situated behind this, and lying over a tract of cartilage, is a small, circular, dentigerous

\* No basibranchials are to be seen beneath the dentigerous plate in the specimen examined; they may have been removed in the preparation of the skull, or possibly their absence is to be explained by the basibranchial cartilages failing to ossify.

bone. Projecting downward from each second hypobranchial is a stout process, similar to that which occurs in the same position in *Osteoglossum* and *Heterotis*. The epipharyngeal teeth of each side are disposed in two contiguous patches.

The foregoing description of the skull of *Pantodon*, read in relation with the summary of the features of the skull in the Osteoglossidæ, points unmistakably towards the existence of a close alliance between the Pantodontidæ and the Osteoglossidæ. The superficial bones of the skull of *Pantodon* are not sculptured, it is true; and the confluence of the right and left premaxillæ is suggestive of the Mormyridæ rather than of the Osteoglossidæ: but, taking the skull as a whole, the evidence is fairly convincing.

The nasals are large and are incorporated into the cranium, and although they do not meet in a median suture as do the nasal bones of the Osteoglossidæ, they resemble these in being suturally united with the anterior edges of the frontal bones. The meeting of the parietal bones in the median line, the smallness of the mesethmoid, the failure of the eye-muscle canal to open posteriorly, the absence of air-vesicles in the hinder part of the cranium, the bounding of the side of the gape by the large maxillary bone, and the absence of a surmaxilla, are characters common to *Pantodon* and the Osteoglossidæ; and—strongest evidence of all—the entopterygoid of *Pantodon* articulates with a lateral peg of the parasphenoid in a manner unknown in any fishes but the Osteoglossidæ. In the great development of the lingual dentition, in the toothing of the parasphenoid and vomer, and in the fusion of the palatine with the ectopterygoid, *Pantodon* bears a closer resemblance to *Osteoglossum* and *Arapaima* than does *Heterotis* to these; but in the absence of a subopercular, and in the want of a roof to the posterior temporal groove, *Pantodon* departs from *Osteoglossum* and *Arapaima*, and approaches *Heterotis*.

Peters, in the original description of *Pantodon* (*l. c.* p. 200), placed the genus in a special subfamily, the Pantodontes, which he intercalated between two other subfamilies, the Hyodontes (*Hyodon*) and the Osteoglossa (*Heterotis*, *Arapaima*, *Osteoglossum*), the three subfamilies constituting the family Osteoglossidæ. Günther ('Study of Fishes,' 1880, p. 653) raised the subfamilies of Peters to family rank, making them the Hyodontidæ, Pantodontidæ, and Osteoglossidæ. Boulenger, in his



recent classificatory scheme of Teleostean fishes (Ann. Mag. Nat. Hist. (7) xiii. 1904, p. 164), has placed the Pantodontidæ and the Osteoglossidæ together, but has separated the Hyodontidæ from them on account of the large size of their supratemporal bone.

From a study of the skull of *Hyodon* (see Journ. Linn. Soc., Zool. xxix. 1904, pp. 206-210), I am disposed to doubt whether any close affinity exists between the Hyodontidæ on the one hand and the Pantodontidæ and Osteoglossidæ on the other; but the results of the present investigation fully justify the action taken by the ichthyologists named in closely associating the Pantodontidæ with the Osteoglossidæ.

#### PHRACTOLÆMIDÆ.

##### PHRACTOLÆMUS ANSORGII.

The family Phractolæmidæ (sole genus *Phractolæmus*) is described by Boulenger (Proc. Zool. Soc. 1901, i. pp. 5-7) as occupying a position intermediate between the Osteoglossidæ and the Clupeidæ. This is the reason why the consideration of the skull of *Phractolæmus* is taken here: as will be seen later, the skull bears no close resemblance to that of either family. The skull examined is that belonging to a skeleton in the British Museum marked "*Phractolæmus Ansorgii*, 1901, 1.28.4, Niger Delta." Some of the more important characters of the skull have already been published by Boulenger in the paper above cited.

The cranium is broad, short, and depressed. The frontal bones are very large, and in the specimen examined the right one overlaps the left. The parietals are small and are widely separated by the supraoccipital, which is broad and short. The transverse commissure of the sensory-canal system passes from parietal to parietal through the supraoccipital bone. Projecting from the side of each exoccipital is a large rib which runs outward and somewhat downward, and is attached by ligament to the pectoral girdle. This cranial rib is in serial order with the trunk ribs (although there are no ribs on the first and second vertebræ), and differs from them in being straighter and shorter. There are no Weberian ossicles, and there are no osseous bullæ for lodgment of cæcal diverticula of the swim-bladder. Opening

backwards at the hind end of the cranium, beneath the parietal and above and external to the epiotic, is a shallow depression hardly worthy of the name of fossa, although the position of the depression is that of the posterior temporal fossa. There is no subtemporal fossa.

The parasphenoid is flat and broad, but becomes narrower immediately beneath the orbits. It possesses no lateral peg for articulation with the hyopalatine arch, and bears no teeth. There are no posterior wings to the parasphenoid, and the eye-muscle canal does not open behind. The vomer is an edentulous thin plate of bone, square in shape and tilted up in front, and movably hinged to the front of the parasphenoid. The most obvious part of the mesethmoid is a bar of bone with a concave anterior edge, set transversely across the anterior ends of the frontal bones. In addition to this, however, is a stout endosteal part which can be seen from the front of the skull only, and which extends downward to the posterior end of the vomer.

The hyopalatine arch articulates with the cranium by a single head, and articulates with the prefrontal just lateral of the junction of the vomer with the parasphenoid. The palatine extends as a thin rod of bone some distance in advance of this. The post-temporal is nearly triangular in shape, but with a notch in front which separates the epiotic limb from the supratemporal limb. There is no opisthotic limb. The nasal bones are not recognisable. Around the eye are five bones—two small rectangular supraorbitals, one postorbital of moderate size, one suborbital, considerably larger, and in advance of it and of about the same size is another suborbital which nearly touches its fellow of the opposite side below the extreme front part of the head.

The opercular bone articulates in the usual manner with a posterior head of the hyomandibular, and below it is a subopercular of about one-sixth its size. The number of branchiostegal rays is three. The preopercular is small, barely larger than the subopercular, but its relations are perfectly normal: *e. g.*, it receives the sensory canal from the squamosal, it is attached by fibrous tissue to the outer surface of the hyomandibular, and its posterior edge overlaps the front of the opercular bone. The greater part of the preopercular is concealed by the postorbital bone.

The interopercular is remarkably large, of about twice the size of the opercular bone; it extends well forward, its pointed anterior extremity nearly reaches the front of the head, and there is a considerable overlapping of the right and left interopercular bones beneath the head. Along the upper edge of the interopercular, and concealed by the overlapping lower edge of the suborbital plate, is a branching sensory canal received from the lower end of the preopercular. The interopercular is thus here performing the function of the missing horizontal limb of the preopercular. This is the only instance known to me in which the sensory canal passes through the interopercular bone: even in *Lepidosteus*, in which the interopercular is situated at the front of the preopercular, the canal does not pass across the interval between the preopercular and the back of the mandible through the interopercular bone, but through the skin (see Collinge, Proc. Birm. Phil. Soc. viii. 2, 1893, p. 265 and pl. 8).

Although the mouth-parts are extremely specialised, the bounding of the gape above is effected, as in the less specialised fishes generally, by the premaxillaries mesially and by the maxillaries laterally. The mouth is very remarkable in form, and is described by Boulenger (*l. c.* p. 6) as "small, probosciform, capable of being thrust forward, when at rest folded over and received into a depression on the upper surface of the head." This depression faces upwards, and is bounded in front by the anterior suborbitals and behind by the mesethmoid. When the mouth is withdrawn, the maxillæ lie against the front of the mesethmoid, and rest on the ledge formed by the front of the vomer; but when the mouth is protruded, a large tract of skin intervenes between the maxillæ and the mesethmoid.

The mouth-skeleton, when the mouth is extruded, is almost detached from the other parts of the skull. It forms a ring of bones around the mouth-opening. Each maxilla is slender, curved into an irregular semicircle, the lateral (*i. e.* the morphologically posterior) extremity being expanded and attached by fibrous tissue to the outer surface of the upper extremity of the dentary. The two maxillæ nearly meet in the median plane of the head, and are connected with one another by fibrous tissue. The two premaxillæ are set immediately in front of the mesial ends of the maxillæ; they have the form of flat, triangular plates of bone, and, being small, they support only the upper part of the

mouth-border, leaving the lateral parts of the maxillæ to support the sides. Each mandibular ramus consists of a slender horizontal part, with a large process upstanding from near the symphyseal end, somewhat as in the case of *Gonorrhynchus*, but more aberrant from the normal proportions. The upstanding parts of the two rami together form a semicircle as viewed from the front, and support the lower part of the border of the gape. At their symphyseal ends the rami are loosely united by fibrous tissue, and each bears near its symphyseal end a stout, short, conical tooth. These two are the only teeth which the animal possesses; it is not clear what purpose they serve, for they have no hard structure opposed to them against which they might bite.

The quadrate is thrust forward far in advance of its normal position, and the union between the quadrate and mandible is effected in such a manner that the ring of bones surrounding the mouth-opening is freely movable in every direction. The hypohyal is large, and single on each side; there is no descending process of the second hypobranchial; the first basibranchial is unossified.

Even if one dismisses from consideration such aberrant features as those of the mouth-bones, the preopercular and interopercular bones, and the suborbital bones, one cannot recognise in the skull of *Phractolæmus* any characters that might be described as "Osteoglossid." On the other hand, one notes that the nasal bones are not incorporated into the cranium, the parietal bones are separated, the mesethmoid and subopercular bones show no sign of reduction, there is no lateral peg of the parasphenoid for articulation with the hypopalatine arch, there is no lingual nor entopterygoid dentition, the hypohyal is large, there is no descending process of the second hypobranchial, and the branchiostegal rays are as few as three in number.

Comparison of the skull of *Phractolæmus* with that of the Clupeidæ is equally unproductive of positive results, for *Phractolæmus* has no diverticula of the swim-bladder in its pro-otic and squamosal bones, no temporal foramen, no pre-epiotic fossa, no auditory fenestra, no fontanelle between the anterior ends of the frontal bones, no posterior wings to the parasphenoid, no posterior opening to the eye-muscle canal, and no surmaxillæ.

It is to be noted, however, that in respect of all the characters just mentioned, and in the fewness of the branchiostegal rays, in



the reduction of the dentition, and in the forward dislocation of the quadrate, *Phractolæmus* resembles *Chanos*. In *Chanos* the relations of the quadrate to the mandibular ramus are normal, but in consequence of the modification of the mouth-parts the quadrate is so far thrust forward as to have parted from the metapterygoid, a most unusual condition. The premaxillæ of *Chanos* are thin scales, like those of *Phractolæmus*; these alone bound the gape above, but if *Chanos* were capable of opening its mouth as widely as *Phractolæmus*, the hinder parts of the maxillæ would bound the sides of the gape.

The main objections to the association of *Phractolæmus* with *Chanos* lie in the possession by the latter of a strongly developed horizontal limb of the preopercular, a fully roofed posterior temporal fossa of large size, backwardly directed spines projecting from the squamosal, supraoccipital, and exoccipital bones, an ossified first basibranchial, and two hypohyals on each side, and in the small size of its vomer. These objections are not insuperable, however, and the resemblance between the skulls of *Phractolæmus* and *Chanos*, though possibly due to "Convergence," is sufficiently suggestive to warrant the undertaking of a comparative study of the other parts of the body of these fishes by any one having the necessary time and material at his disposal.

## EXPLANATION OF THE PLATES.

## PLATE 30.

- Fig. 1. *Osteoglossum Leichardti*. Dorsal view of cranium.  
 2. " " Side view of cranium.  
 3. " " Back view of cranium.  
 4. " " Right side of skull.  
 5. " " Hyopalatine arch of left side, with opercular bones and mandible, mesial aspect.

## PLATE 31.

- Fig. 6. *Heterotis niloticus*. Dorsal view of cranium.  
 7. " " Side view of cranium.  
 8. " " Back view of cranium.  
 9. " " Right side of skull.  
 10. " " Hyopalatine arch of left side, with opercular bones and mandible, mesial aspect.  
 11. " " Occipital half-vertebra, posterior view.



## PLATE 32.

- Fig. 12. *Arapaima gigas*. Dorsal view of cranium.  
 13. " " Side view of cranium.  
 14. " " Back view of cranium.  
 15. " " Right side of skull.  
 16. " " Hyopalatine arch of left side, with preopercular bone and mandible, mesial aspect.

*Abbreviations employed in the Figures.*

<i>al</i> ... alisphenoid.	<i>or</i> ... orbitosphenoid.
<i>an</i> ... angular.	<i>p</i> ... parietal.
<i>bo</i> ... basioccipital.	<i>pl</i> ... palatine.
<i>c</i> ... centrum of occipital half-vertebra.	<i>pm</i> ... premaxilla.
<i>c'</i> ... centrum of the vertebra behind <i>c</i> .	<i>pof</i> ... postfrontal.
<i>cor</i> ... circumorbital bones.	<i>pop</i> ... preopercular.
<i>ct</i> ... cartilage.	<i>pp</i> ... parasphenoidal peg for articulation with the entopterygoid.
<i>d</i> ... dentary.	<i>prf</i> ... prefrontal.
<i>ecar</i> ... ectosteal articular.	<i>pro</i> ... pro-otic.
<i>ecp</i> ... ectopterygoid.	<i>ps</i> ... parasphenoid.
<i>enar</i> ... endosteal articular.	<i>pt</i> ... post-temporal.
<i>enp</i> ... entopterygoid.	<i>ptf</i> ... posterior temporal fossa.
<i>eo</i> ... exoccipital.	<i>q</i> ... quadrate.
<i>ep</i> ... epiotic.	<i>r</i> ... rib.
<i>f</i> ... frontal.	<i>s</i> ... teeth on lingual surface of dentary.
<i>hm</i> ... hyomandibular.	<i>sar</i> ... sesamoid articular.
<i>im</i> ... intermuscular bone.	<i>soc</i> ... supraoccipital.
<i>iop</i> ... interopercular.	<i>sop</i> ... subopercular.
<i>me</i> ... mesethmoid.	<i>sq</i> ... squamosal.
<i>mpt</i> ... metapterygoid.	<i>st</i> ... supratemporal.
<i>mx</i> ... maxilla.	<i>stf</i> ... subtemporal fossa.
<i>n</i> ... nasal.	<i>sy</i> ... symplectic.
<i>op</i> ... opisthotic.	<i>v</i> ... vomer.
<i>opc</i> ... opercular.	





